THE DYNAMICS OF A DIATOM BLOOM[1]

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Phytoplankton cells respond so rapidly to their environment that conventional methods of studying their populations fail to reveal many of the more subtle and more interesting aspects of their dynamic ecology. This is particularly true of surveys in which observations are made at intervals of weeks or months, where the very use of the term "the phytoplankton population," when carried over from one set of observations to the next, implies more knowledge than is available. It is also true of productivity measurements made over 24 hours or the daylight portion of a day, since Rodhe (personal communication), Doty and Oguri (1957), Yentsch and Ryther (1957) and others have shown that the plants vary in their composition and react differently to their environment at different times of the day. To study such phenomena it is obviously necessary to make intensive observations at very frequent intervals throughout one or more days on single, isolated populations.

This type of study presents obvious difficulties. The average natural population is sparse enough so that its properties can be measured only with rough accuracy, and the errors of such measurements may be larger than the changes in the organisms and their environment which are under investigation. Some insight into these problems may be had by studying cultures, but the difficulties of growing organisms under completely natural conditions need no elaboration here. A compromise may be reached, however, by working with a dense phytoplankton bloom. Here natural populations may be studied under their natural growing conditions and very rapid responses of the organisms to changes in their physical or chemical environment may be detected and measured.

The authors encountered such a diatom bloom in a small tidal creek on the south shore of Long Island, N. Y., in June, 1957. The following report will describe the studies of this bloom which were made over a 40-hour period including two days and one night.

Description of the Area

Senix Creek is approximately one mile long, tapering from a width of about 300 meters at its mouth to less than 10 meters at its upper end in the town of Center Moriches. Our observations were made about halfway up its length where the water depth is approximately one meter. Underlying this shallow body of water is a thick deposit of black, organic muck which discharges H_2S gas when disturbed.

There is no river or other obvious source of fresh water to Senix Creek except for local runoff. The latter was negligible in the early summer of 1957 due to

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abnormally low rainfall (none whatever during the month of June). This drought was undoubtedly an important contributory factor to the existence of the diatom bloom, since it helped to maintain the salinity at a moderately high level in the estuary and also reduced flushing action so that the latter did not greatly influence the population at the time and place of our observations.

While many of the tributaries to Moriches Bay receive large quantities of pollutants from duck farms which line their shores (see Ryther, 1954), there is no such direct source of enrichment to Senix Creek. The origin of the nutrients which gave rise to the phytoplankton bloom in question was not investigated. They presumably resulted either from domestic pollution from Center Moriches and the residences located along the banks of the creek, or from an invasion of water from one of the other, heavily polluted estuaries via Moriches Bay (*i.e.*, Forge River located just ½ mile from Senix Creek at their respective mouths).

Methods and Procedure

The studies were initiated at sunrise on June 26, with the plan to make observations hourly during the day and less frequently at night for 24 hours. Unfortunately, the day was foggy and partially overcast, and it seemed doubtful that we would be able to observe phenomena associated with high incident light intensities. Consequently we continued the study for the daylight portion of a second day, when the sky was clear.

Incident radiation was measured at one-hour intervals throughout the day with a GE radiation meter. Light penetration was measured with a submarine photometer constructed from a Weston photronic cell. Water level, measured with an improvised tide gage, was also recorded hourly during the day, less frequently at night. At these same time intervals water samples were collected in a bottle equipped with a siphon which permitted the sample to enter through a tube running to the bottom of the bottle and the air to escape through a tube extending to the surface of the water. In this way samples for gas analysis were not contaminated by bubbles. As the bottle filled it was slowly lowered from the surface to the bottom, thereby obtaining an integrated sample of the one-meter water column. Immediately after collection, the water temperature was taken and an aliquot of the sample was siphoned into a 150-ml. glass-stoppered bottle and analyzed for dissolved oxygen using the Pomeroy-Kirschman-Alsterberg modification of the Winkler method (see APHA, 1955). The pH of the sample was measured with a Coleman pH meter, and a 100-ml. aliquot was withdrawn and millipore-filtered for subsequent pigment analysis using the method of Richards with Thompson (1952) as modified by Creitz and Richards (1955). Pigments were computed using the nomographs prepared by Duxbury and Yentsch (1956).

Every two hours during the day, additional aliquots were siphoned into four 150-ml. bottles, one of which was darkened with black tape. These were then suspended in the water, the three transparent bottles at depths of 0, 0.5 and 1.0 meter. After two hours, the bottles were removed and their dissolved oxygen concentration determined.

At high and low water each day, as determined from the tide gage, additional samples were collected from the surface and from a few centimeters above the bottom. These were returned to the laboratory where they were analyzed for

salinity and used for total phytoplankton counts. At 10:30 on June 27 a single sample, taken from the whole water column, was frozen and subsequently analyzed for phosphorus and nitrogen fractions.[2]

Observations and Results

a. The phytoplankton

The phytoplankton population in Senix Creek consisted predominantly of centric diatoms, principally *Chaetoceros simplex*, *Thalassiosira nana*, and *Skeletonema costatum*. Other species present in abundance were the naviculoid diatom *Phaeodactylum tricornutum* (*Nitzschia closterium* forma *minutissima*), the green flagellate *Carteria excavata*, and the dinoflagellate, *Prorocentrum minimum*. The concentration of diatoms alone ranged from 61 to 109 million cells per liter. In addition there were observed large numbers of small coccoid cells, 1–2 μ in diameter, which were not identified but were either bacteria, blue-green or green algae. They bore some resemblance to the green alga, *Nannochloris atomus*, which was formerly present throughout Moriches Bay and its tributaries in concentrations exceeding 10^{10} cells per liter prior to the opening of Moriches Inlet in 1954. At that time the growth of *Nannochloris*, which virtually replaced the normal estuarine plankton flora, was attributed to high concentrations of pollutants originating from the duck farms, low salinities, and high temperatures (Ryther, 1954). These conditions still persist near the sites of pollution in the estuaries of Moriches Bay (for example in the Forge River and Seatuck Cove), where the phytoplankton was dominated by green algae and the water was a distinct green color in contrast to the rich brown color of the water in Senix Creek.

Table I

The vertical distribution of salinity and diatoms in Senix Creek

		Salinity (‰)	Diatoms (10^6/liter)
June 26	High tide		
	surface	11.94	92.8
	bottom	13.48	80.6
	Low tide		
	surface	10.22	109.0
	bottom	13.10	82.0
June 27	High tide		
	surface	11.73	82.8
	bottom	14.54	61.3
	Low tide		
	surface	11.64	79.5
	bottom	16.53	61.3

The small microorganisms in Senix Creek, though about ten times as numerous

[2] Analyses were made by methods described in the following references: inorganic phosphorus (Robinson and Thompson, 1948); total phosphorus (Harvey, 1948); ammonia (Riley, 1953); nitrite (Rider and Mellon, 1946); nitrate (Mullin and Riley, 1955).

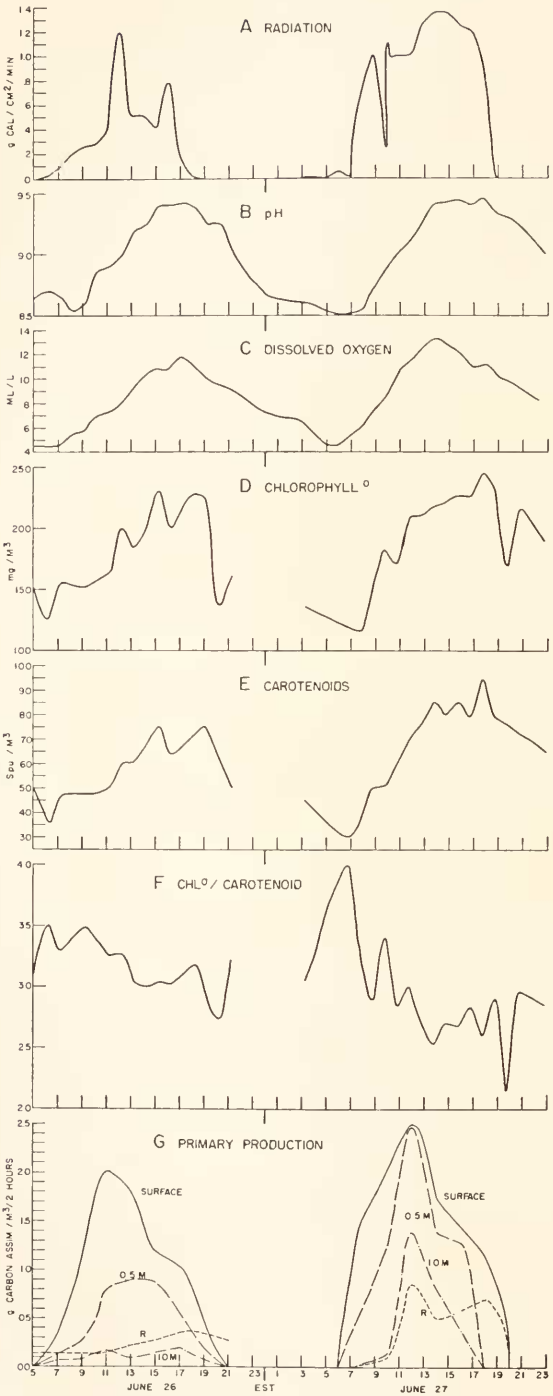

FIGURE 1. Variables measured in Senix Creek between 05:00, June 26 and 20:00, June 27.

as the diatoms, were probably insignificant in terms of total biomass since their cell volume is several hundreds of times smaller than that of the average diatom.

b. The physical environment

Figure 1A shows the incident radiation for the two days. The total daily radiation, obtained by integration of these curves, was 300 gram-calories/cm². on June 26 and 740 gram-calories/cm². on June 27.

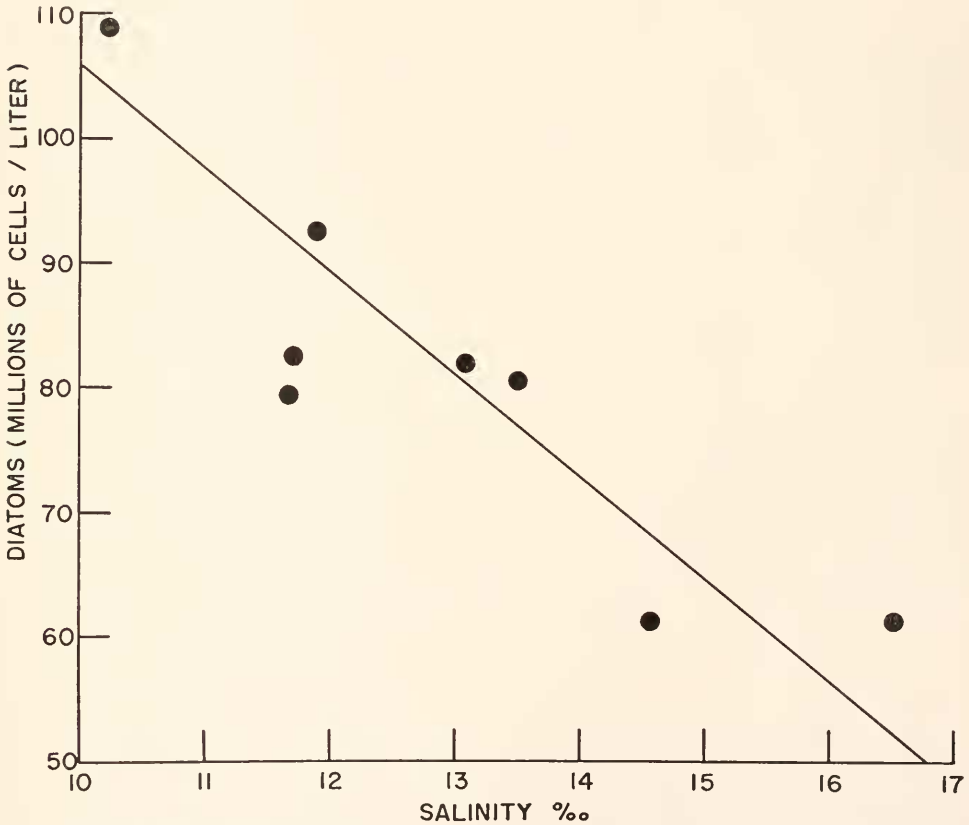

FIGURE 2. The relation between salinity and total diatom concentration, showing least squares line (R = −.875). Data from Table I.

The tidal influence in Senix Creek is extremely small. The range between high and low water on both days was approximately seven inches. Salinities ranged from 10–15 ‰ and showed no obvious correlation with the stage of the tide. However, salinities at the bottom were slightly higher than those at the surface, and salinities were higher the second day of observations than on the first (Table I).

Diatom counts were slightly lower at the bottom than at the surface and lower at both depths on the second day. Again there was no obvious relation to the tide,

but there was a good inverse correlation ($r = -0.875$) between the diatom concentration and the salinity (Fig. 2). This correlation suggests that the diatom population did not change over the two-day period as a result of growth or death, but that the population was being diluted slowly with water from Moriches Bay, where the salinity ranged from 20 to 25 ‰ and diatom concentrations were generally less than one million cells per liter.

c. Dissolved oxygen and pH

Both pH and dissolved oxygen behaved in essentially the same manner, as may be seen by comparing Figures 1B and C. However, the high pH attained in the late afternoon of both days was maintained for several hours whereas the oxygen concentration reached its peak at the same time but then began to decline immediately. Water temperatures (which are not shown) ranged from 25° C. to 28° C. during the two-day period. Assuming a mean salinity of 12‰, the water was approximately 90% saturated with oxygen at daybreak, about 270% saturated at 14:00 on June 27. Despite this supersaturation, there did not appear to be a significant loss of oxygen to the air by diffusion since the decrease in oxygen concentration at night by respiration appears to have occurred at a constant rate. If appreciable loss by diffusion had occurred, this would have been dependent upon the oxygen concentration, and the decrease due to both causes (respiration and diffusion) would have been non-linear.

The pH reached a minimum of about 8.5 early in the morning and a maximum of almost 9.5 in the afternoon. Presumably at its maximum, no free CO_2 was available and any further photosynthesis was dependent upon bicarbonate or carbonate ions. Unfortunately no measurements were made of CO_2 in any of its fractions, nor may these values be calculated from pH, salinity, and temperature for these estuarine conditions as they may for either fresh or sea water. Again the regular behavior of the pH curve with time, shown in Figure 1C, indicates that CO_2 diffusion from air to water was negligible in comparison to the changes caused by photosynthesis and respiration.

d. Plant pigments

Figure 1D shows the concentration of chlorophyll *a* in the composite samples taken during the two-day period. Since the cell counts were not made on the same samples, it is not possible to represent chlorophyll on a cellular basis. The chlorophyll concentration in the water ranged from 116 to 245 mg./m^3., about a two-fold variability. Although the highest concentrations coincided on both days with low water, the connection between these factors is probably fortuitous. Certainly the variations in the pigment concentration are far greater than the observed differences in the diatom counts, caused by tidal fluctuations or otherwise. Despite the somewhat erratic distribution of the pigment concentration, it is still obvious that the chlorophyll increased gradually throughout the day, reaching its peak at about sunset, after which it decreased rapidly throughout the night until daybreak.

Similarly the plant carotenoid pigments increased during the day and decreased at night (Fig. 1E). Both chlorophyll and carotenoids increased to higher values on the second day, which differed from the first primarily in the amount of incident

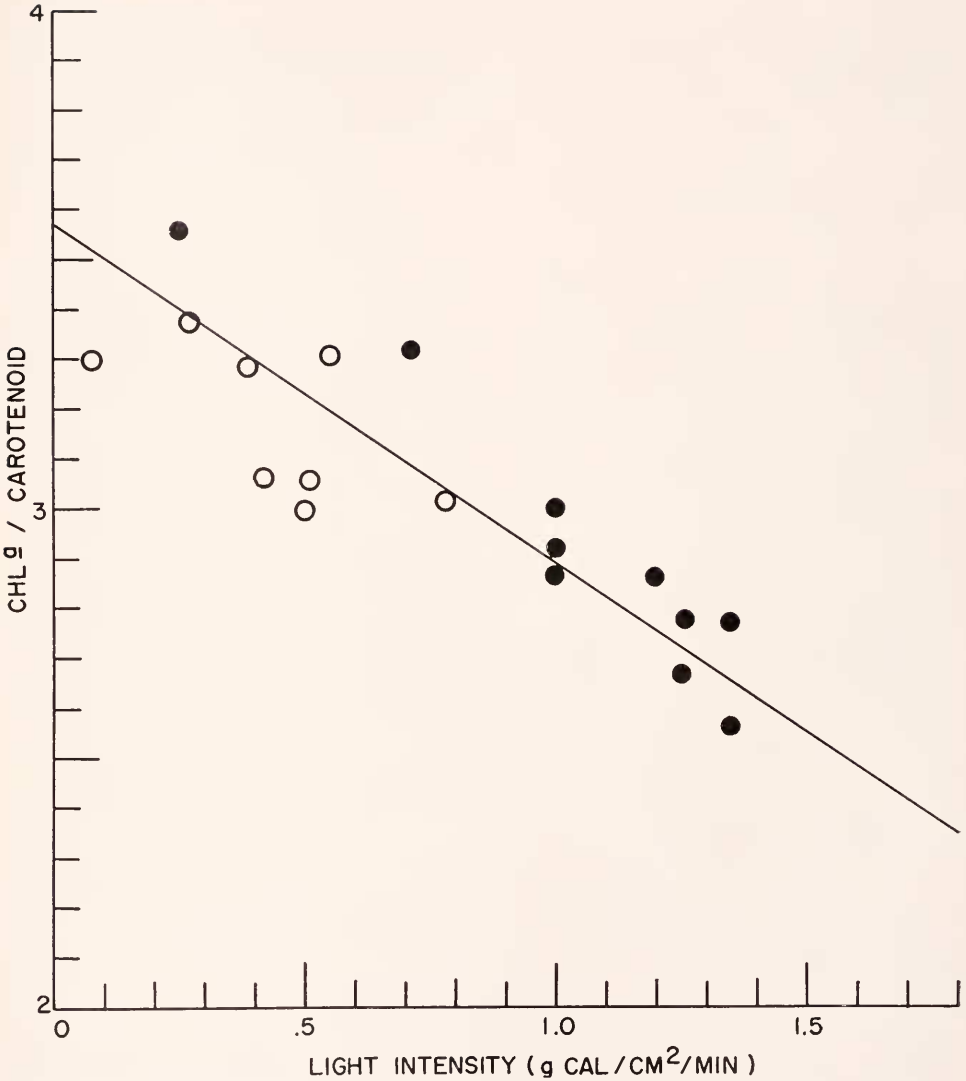

FIGURE 3. The relation between incident radiation and the ratio chlorophyll *a*:carotenoid pigments in the diatom population. Open circles, June 26. Closed circles, June 27.

radiation. The carotenoid pigments ranged on June 27 from a minimum of 30 SPU [3] at 05:45 to 95 SPU at 17:45, more than a three-fold variation.

The ratio chlorophyll *a*:carotenoid pigments (Fig. 1F) decreased throughout the daylight periods of both days from maximum values observed at sunrise, the more rapid decrease on June 27 again correlated with the greater incident radiation

[3] The spectrophotometric analysis of carotenoid pigments has not been standardized in absolute units and they are reported in specific pigment units after Richards with Thompson (1952). One SPU, however, is closely equivalent to one milligram of pigment.

on that day. Figure 3 shows the inverse relationship which was found between the intensity of solar radiation and the chlorophyll : carotenoid ratio. The variations in this ratio are the result of a differential effect of light on pigment synthesis and decomposition where the chlorophyll changes are of much greater magnitude than are the carotenoid changes (Yentsch and Scagel, unpublished). The significance and interpretation of the magnitude and changes in this ratio will be discussed in the final section of this paper.

c. Primary production

Primary production was calculated by the following three methods: (1) the *in situ* changes of oxygen in the water, (2) the "light-and-dark-bottle" oxygen measurements, (3) the "chlorophyll-radiation" method of Ryther and Yentsch (1957). The inability to measure or calculate total CO_2 prevented the use of pH changes or the C^{14} method for this purpose.

On June 26, the dissolved oxygen in the integrated sample collected over the one-meter water column increased from a minimum of 4.5 ml./liter at 07 :00 hours to a maximum of 11.8 ml./liter at 17 :00 hours, a difference of 7.3 ml./liter. If an assimilatory quotient of 1.25 is used, this change in oxygen is equivalent to a carbon fixation of 3.15 grams/m^2./day. As mentioned earlier, the decrease in oxygen at night appears to have been due almost entirely to respiration. This loss was equivalent to 0.5 ml. oxygen/liter/hour. During the 10 hours of daylight, if respiration occurred at the same rate, this would account for a total of 5.0 ml. O_2/ liter or 2.15 grams carbon/m^2./day. Adding this respiratory loss to the observed net production of 3.15 grams carbon/m^2./day gives a total or gross production of 5.20 grams carbon/m^2./day.

In the same way production was calculated for June 27, the net change in oxygen being equivalent to assimilation of 3.8, the respiration loss 1.7 and the gross production 5.5 grams carbon/m^2./day.

The two-hour "light-and-dark-bottle" experiments which were described above were also used to calculate gross and net production. The differences between the oxygen concentration of the light bottles at 0, 0.5, and 1.0 meter and that of the accompanying dark bottle over the two-hour experimental periods, converted to carbon assimilation as above, are shown in Figure 1G. The carbon equivalent of respiration for the same two-hour periods was obtained from the difference between the oxygen content of the water at the beginning of the two-hour period and that of the dark bottle. These curves were integrated to obtain daily photosynthesis at each depth and daily respiration. These values in turn were plotted against depth and integrated to give daily photosynthesis and respiration beneath a square meter of surface. Gross photosynthesis for June 26 calculated by this method was 3.5, respiration was 1.7 and net photosynthesis 1.8 grams carbon/m^2./ day. On June 27 the values were 6.2, 2.8 and 3.4 grams carbon/m^2./day for gross production, respiration and net production, respectively.

The *in situ* oxygen changes at night appeared to indicate a constant respiration rate of 0.5 ml. O_2/liter/hour, and this, as described above, was used to correct the net *in situ* change observed in daylight to give gross production. An examination of the two-hour bottle experiments during the day shows that, when measured in this way, respiration was by no means constant but varied roughly in proportion to the rate of photosynthesis. On June 27, for instance, the respiratory rate ranged

from 0.06 ml./liter/hour in the early morning to about 1.00 ml./liter/hour at midday. These measurements, though somewhat crude, emphasize the need for a reconsideration of the tacit assumption made by most ecologists that respiration measured at night, or for long periods in dark bottles, is the same as that which occurs in the light in conjunction with photosynthesis.

The third method for estimating production is that developed by Ryther and Yentsch (1957). This method requires measurement of the concentration of chlorophyll *a*, the total daily incident radiation, and the extinction coefficient of visible light in the water. The latter was determined by the measurement of light penetration to one meter with a submarine photometer at 13:30 hours on June 26. The extinction coefficient (k) so determined was 4.0. Use of this method required an obvious over-simplification, since the chlorophyll *a* concentration, as has been pointed out, varied throughout the day. A mean value of 200 mg. chl*a*/m^3. was used for the calculation for both days, and this was assumed to be uniformly distributed over the one-meter water column. The resulting values for gross production were 3.2 and 5.1 grams carbon/m^2./day for June 26 and 27, respectively.

The results obtained by these three methods are summarized in Table II. They show rather good agreement except for the values obtained by *in situ* oxygen changes on June 25 which are almost twice as high as those obtained by the other

TABLE II

Primary production in Senix Creek on June 26 and June 27, as measured by three methods (grams carbon assimilated/m.^{2}/day)

Method	Gross	Net (day)	Net (24 hrs.)	Gross	Net (day)	Net (24 hrs.)
In situ O_2	5.3	3.15	0	5.5	3.8	0
L-D bottle O_2	3.5	1.76	—	6.2	3.4	—
Chlorophyll	3.2	—	—	5.1	—	—

two methods. It should be pointed out that the net production values which have been discussed refer to this process during the daylight hours only. The only estimates over a 24-hour period which can be made are based upon the *in situ* oxygen changes (and pH changes) which clearly reflect a net production for this period of zero. Finally, the net changes observed *in situ* and *in vitro* are acknowledged as representing changes brought about by the whole community including animals and bacteria, and do not characterize the plant population alone.

The efficiency of production on the two days may be roughly estimated by taking the median of the values obtained by the three methods for daily gross production, 3.5 and 5.5 grams carbon/m^2. on June 26 and 27, respectively. If the assumption is made that 50% of the photosynthetic production is carbon and has a heat of combustion of 5.5 k cal./gr. (see Krogh and Berg, 1931), and further that half the incident radiation may be used for photosynthesis, the efficiency may be calculated as:

$$\text{a) June 26} \quad \frac{3.5 \times 2 \times 5{,}500}{1{,}500{,}000} = 2.6\%$$

$$\text{b) June 27} \quad \frac{5.5 \times 2 \times 5{,}500}{3{,}700{,}000} = 1.6\%$$

f. The physiology of the bloom

There are several indications that the diatom population in Senix Creek was a non-growing one which had exhausted its supply of available nutrients and was able to subsist at a basal level, photosynthesizing just enough during the day to compensate for its metabolic requirement over a 24-hour period. This is best illustrated by the *in situ* oxygen and pH values, in which the net oxygen produced and CO_2 assimilated during the day are exactly compensated by the reverse processes at night. Further evidence of this is the fact that the concentration of diatoms remained unchanged over the 48 hours of observation except where such changes are attributable to tidal flushing.

The evidence that the bloom was nutrient-limited is somewhat sparse and indirect, but rather convincing. At 10:30 hours on June 27 an integrated water sample was collected and frozen. This was later analyzed for nitrogen and phosphorus fractions at the Woods Hole Oceanographic Institution. The results of these analyses are given below.

	μg Atoms/liter
$NO_2- + NO_3-$	3.40
NH_3+	1.49
PO_4	3.80
Total P	16.0

A photosynthetic rate of 5.5 grams carbon/m².day in a one-meter water column represents a requirement of 460 μgA carbon/liter/day. As Redfield (1934) and others have pointed out, marine phytoplankton assimilate carbon, nitrogen and phosphorus at an atomic ratio closely approaching 100:15:1. This rate of carbon assimilation is therefore equivalent to a daily requirement of 71 μgA/liter of nitrogen and 4.6 μgA/liter of phosphorus. Thus, the concentrations of these elements in the mid-morning of June 27 represented no more than a fraction of a day's supply of either nitrogen or phosphorus. These calculations were based upon the requirement of normal cells. Photosynthesis may of course continue after nitrogen and phosphorus are exhausted with the storage of carbohydrates and lipids. This is presumedly what was happening in this population, the cells using these stored materials to satisfy their metabolic requirements at night. Further studies of this type of population, with emphasis placed upon the diurnal cycle of nutrients, would be particularly interesting.

The behavior of the plant pigments is a further indication of the physiological condition of the population. The fact that both chlorophyll *a* and the carotenoids were synthesized during the day and decomposed at night signifies that the plants were drawing upon their cellular reserves to maintain themselves in the dark. When nutrients are available, this does not occur; in fact, chlorophyll may be synthesized in the dark under favorable growing conditions if the cells have sufficient respiratory reserves (Harvey, 1953).

Experiments in this laboratory (Ketchum *et al.*, 1958) and elsewhere have shown that both chlorophyll *a* and the carotenoid pigments decrease in diatoms in response to nitrogen, phosphorus or iron deficiency or excessive illumination. This nutritional chlorosis results in a more rapid decomposition of chlorophyll than carotenoid pigments. As the day progressed the pigment ratio decreased, presumably in part because of nutrient exhaustion which was hastened by greater demands of photosynthesis at high light intensities (Fig. 3).

The picture which emerges from these various bits of evidence, then, is that of a static diatom bloom of great magnitude, its nutrient supply exhausted or at least reduced to the level where growth could not occur. Yet it was not a dying population, except insofar as physical forces tended to disperse it. It was capable of carrying out organic synthesis at a rate some 10–100 times that of normal plankton communities, drawing upon these materials for its metabolic requirements much the same as a mature animal maintains a balance between its assimilation and metabolism.

It would appear, then, that populations of phytoplankton such as we have described here, though not actively growing, are not necessarily dying either. They are merely living in a different growth phase, a condition in which they may persist for long periods of time if they are not destroyed or dispersed by external factors. Perhaps in diatom populations, as elsewhere, the bloom of maturity may outlast the bloom of youth.

Summary

1. A dense population of planktonic diatoms was studied over a 40-hour period in a small tidal creek on the south shore of Long Island, New York.

2. Measurements were made at frequent intervals of incident radiation, light penetration, salinity, temperature, dissolved oxygen, pH, concentration of diatom cells and their pigments, and dissolved inorganic nutrients. Photosynthesis and respiration were measured by oxygen changes in bottle experiments and estimated from *in situ* oxygen changes and from chlorophyll *a* and radiation.

3. The plankton community appeared to be nutrient-limited and consisted of a static, non-growing diatom population which was being slowly diluted by tidal action. This was indicated by the diatom counts, the behavior of their pigments (which increased throughout the day and decreased during the night) and the concentration of available plant nutrients.

4. Rates of primary production measured by three methods showed good agreement, the values ranging from 3.2 to 5.3 grams carbon assimilated/m^2./day on June 26, from 5.1–6.2 on June 27. Total incident radiation for the two days was 300 and 740 gram calories/cm^2./day, respectively, and the efficiency of the photosynthetic utilization of visible radiation for the two days was estimated at 2.6% and 1.6%, respectively.

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